

THE RATE OF WATER PROPULSION BY THE CALIFORNIA MUSSEL

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Numerous investigators have approached by means of various experimental techniques the problem of the volume of water which may pass in a given time through the mantle cavity of lamellibranch mollusks. The establishment of an approximate, or even a minimum figure for the volume of water pumped per day by any of the many marine plankton-feeding animals would be of interest to physiologists who may be concerned with nutritional, respiratory, or excretory activities of the animal itself, to planktologists whose problems deal with the numerous factors which influence the numbers and distribution of microscopic plants and animals that may be consumed by the filtering animals, and to oceanographers who seek information regarding biological factors concerned in modifications of the physical and chemical character of both water and bottom in various regions of the sea. In many instances, those who have contributed to our knowledge of the water-filtering and feeding activities of lamellibranchs have been primarily interested in the sanitary and other technical aspects of cultivating oysters and mussels for human consumption. Thus Viallanes (1892) presented approximate figures for the relative rates of filtration of water by French oysters, Portuguese oysters, and mussels. He placed the animals in separate crystallizing dishes upon the bottom of a tank supplied with flowing sea water, keeping initially empty dishes of the same size and design alongside of the experimental ones, in the same tank. At the end of a specified time interval the material which had been filtered from the water by the animals, and either swallowed and later voided as fecal material, or else rejected as pseudofeces directly from gill and mantle surfaces, was collected, dried, and weighed. The weight of filtered material was obtained by subtracting that of the detritus which had settled out of the water by gravity into the control dishes. Viallanes performed similar experiments more critically by dispersing a known quantity of dry clay in a given volume of water, drying and weighing the quantities of clay deposited by the different bivalves after 24 hours. From his first experiment, wherein

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the suspended material naturally present in the sea water was the only available particulate matter, he calculated that his animals (of age = 18 months) filtered water at the following relative rates: French oyster, 1.0; Portuguese oyster, 5.5; mussel, 3.0. The clay experiments, however, showed very different results, which were left undiscussed. Table I shows briefly his results.

Viallanes found that the mucus which was secreted by the mollusks and in which the precipitated clay was incorporated, weighed only 4 per cent of the weight of the whole mass.

Ranson (1926) cites the work of Viallanes and reports briefly his studies of the mechanism of filtration. Both investigators emphasize the importance of the filtering function of lamellibranch plankton- and detritus-feeders to ostreiculturists and to oceanographic science.

TABLE I
Filtration and deposition of suspended clay by Viallanes' lamellibranchs.

Animal	Initial quantity of dry clay	Weight of clay deposited in 24 hours	Minimum volume of water filtered per hr. (our calculation)
	<i>gram/liter</i>	<i>grams</i>	<i>liters</i>
Mussel (18 months)	0.0546	1.768	1.35
Portuguese oyster (18 months)	0.0546	1.075	0.82
French oyster (18 months)	0.0546	0.199	0.015

Criticisms of Viallanes' experiments which must be borne in mind are: (1) in his first experiments with naturally-occurring particulate matter, the portion of the material which had been actually swallowed, the undigested residue of which was finally voided as fecal material, must have undergone changes of various kinds and degrees depending upon the relative rates and processes of digestion in the different species, and have subsequently vitiated the interpretations that were based merely upon relative weights; (2) in both of the experiments, the quantities of detritus or clay which had been removed from the water but still remained in the animals' alimentary tracts were not weighed or considered. Since in each case such small total weights were being measured, this item might have constituted a considerable, though by no means predictable or constant fraction of the total figure.

Galtsoff (1926, 1928*a*, 1928*b*) measured the rate of flow of water through the gill chamber of the American oyster, and calculated the work done by the propelling cilia. He used two methods, one a direct one in which the water issuing from the exhalant chamber was collected in a measuring vessel, the other in which the rate of advancement of a

stream of water flowing from the exhalant chamber through a glass tube was measured by stop-watch. Both methods involved the insertion of a small glass rod between the opened valves to prevent their closing, and placing into the gill cavity a rubber tube, to carry off the discharged water, packing other open spaces around the tube with cotton. Galtsoff (1928*b*) records a maximum figure of about 3.9 liters per hour for the water intake of a single healthy adult oyster three to four inches in length at a temperature of 25° C.; the temperature at which the highest rate of flow occurred was found to be between 25° and 30° C. He points out, and shows by collected data the fact that considerable variations exist in the rate of flow produced by individual oysters. His average temperature-flow rate curve, taken from data collected in the study of many individuals, shows, at temperatures close to 30° C., a maximal rate of about 2.4 liters per hour while at 20° C. the average rate lies close to 2 liters per hour. At temperatures between 24 and 27.9° C., filtration took place at the rate of from 2.5 to 2.9 liters per hour. He points out that the filtering action of the oyster is dependent upon two mutually independent functions, namely the beating of the cilia and the opening and closing of the valves of the shell, the process occurring only when the valves are apart and the cilia beating. His studies showed that the oyster keeps its shell open for an average time of about seventeen hours out of twenty-four. (June to October.)

Numerous attempts have been made to estimate the rate of flow of water through the gill chambers of lamellibranchs on the basis of plankton counts in the water itself, and in the animals' stomachs. The results are, however, not satisfactory because, as Galtsoff (1928*b*) points out, there are daily and seasonal variations in plankton numbers in the water; not all of the diatoms filtered out by the gills are ingested but may be rejected instead. Such experimental work should, however, if carefully controlled, afford minimum figures. It would seem for various reasons probable that most methods used to date might be expected to yield results that are lower than the true figure for the volume of water filtered per day.

Various investigators (see also Galtsoff, 1928*b*) have obtained widely different results for the rate of water-pumping by plankton feeders. Collateral data regarding temperature are, however, not always available. Briefly, the general conclusions may be recorded as shown in Table II.

The inconsistencies which appear from an examination of these figures serve to emphasize the wide variations according to the method used, and the unreliability of the plankton count method. Galtsoff's studies convinced him that as many as 18.9 per cent of phytoplankton

such as the diatoms *Chaetoceros* and *Rhizosolenia*, and the dinoflagellates *Peridinium oceanicum* and *Ceratium* might escape being caught while passing through the gills, and that from 50 to 89 per cent of bacteria present in the water passed the gills of his oysters. Work at this Institution, however, shows that the mussel is quite successful in removing bacteria from water. Thus ZoBell and Landon (1937) demonstrated that the mussel removed about 99.9 per cent of added bacteria from sea water. (See also Fox et al., 1936.)

Without doubt, Galtsoff's direct methods are the most accurate for

TABLE II
Filtration of water by plankton-feeders.

Investigator	Animal	Method	Average rate of filtration (liters per hour per animal)
Grave (1905)...	Oyster	Plankton counts in water and stomachs	0.167
Moore (1913)...	Oyster	Plankton counts in water and stomachs	ca. 1.25
Allen (1914)...	Freshwater mussel	Rubber tube packed into exhalant chamber	1.4
Wells (1916)...	Oyster	Plankton counts in water and stomachs	7.5
Nelson (1921)...	Oyster	Rubber apron dividing inhalant and exhalant chambers	5.7 (but see text below)
Galtsoff (1926, 1928a, b)...	Oyster	Rubber tube packed into exhalant chamber	2.5-2.9 at 24-26.9° C.
Dodgson (1928)	Mussel (<i>Mytilus edulis</i>)	Clearing of suspensions	2.0 (minimum, at 17° C.)
Parker (1914)...	Sponge (<i>Spinosella</i>)	Glass tube tied into osculum	3.2
Damas (1935)...	Cardium	Clearing of mud suspensions	0.1

the measurement of the rate of flow of water through the mantle cavity under the conditions imposed upon the oyster. Needless to say, a question arises in one's mind regarding the possible influences that blocking the valves apart with a glass rod, inserting a rubber tube into the excurrent chamber, and packing the openings in the mantle surrounding the inserted tube with wads of cotton might exert upon the normal feeding and filtering behavior of the animal.

Nelson (1935) refers to earlier efforts to measure the water filtered by an oyster, and to the fact that very diverse results were obtained. He writes, "The introduction of a tube into the cloacal chamber inter-

feres with normal operation of the branchial hearts described by Hopkins and may disturb the visceral ganglion." He adds, "Also, in *Ostrea virginica* much of the water from the right demibranch leaves by an asymmetric chamber on the right side and separate from the cloacal chamber." Using a modification of the rubber apron of Moore (1908), he claims to have measured all the water passed by an oyster, without interfering with its normal activities. He reports the amazing value of 26 liters of water per hour, passed by an oyster 11.5×8.9 cm. in size, at the optimum temperature of 30° C. This is about tenfold the average values found by Galtsoff for the oyster and by ourselves for the mussel. Fresh oyster sperm were found by Nelson to increase markedly the rate of water propulsion by male oysters, while in females no response was observed unless spawning occurred, in which case the filtration-rate was temporarily reduced.

Parker (1914) reports on the strength and volume of water currents produced by sponges. He measured the average height to which the excurrent stream of water might reach when glass tubes of appropriate size were tied securely into an osculum. By measuring the rate at which carmine particles, etc., were carried out of a glass tube of known dimensions, Parker concluded that the sponge *Spinoseella* discharged water from its oscula at a rate of about 4.5 cc. in five seconds, or about 78 liters per day. A colony of *Spinoseella* having as many as twenty oscula might, he concluded, strain in a day more than 415 gallons of water.

Damas (1935) studied the activities of plankton-feeders, especially *Cardium* and other lamellibranch mollusks, with reference to their rôle in the deposition of marine muds. He calculated, on the basis of quantitative observations of the extraordinary rate of deposition of mud pellets by *Cardium*, that 1,000 such individuals produce, on an average, a layer of mud of 0.45 meter in thickness per square meter per year, or 1,250,000 cubic meters of mud per year in the 250 hectares (1 hectare = 10,000 sq. m.; 2.471 acres) colonized by *Cardium* in the roadstead of Zeebrugge.

The question of the natural filtration rate has been approached by Dodgson (1928) and by ourselves under conditions which would seem to simulate more closely those of nature. Dodgson and co-workers, working with the bay mussel, *Mytilus edulis*, at Conway, Wales, prepared turbid suspensions of different substances such as flour, clay, fine silt, and even ordinary muddy river water, in sea water. On the basis of many experiments, Dodgson claims that "end-points," i.e. the time at which the formerly cloudy solutions become quite limpid, could be determined without difficulty, the last traces of turbidity disappearing almost suddenly. At 17° C., mussels placed in turbid suspensions of fine silt,

mud, clay, or flour filtered the water to clarity at estimated minimum rates varying between 1.9 and 2.6 liters per hour per mussel. His average figure of about 2 liters per hour per mussel is expressed as being probably far less than the actual quantity, since, in order to remove quantitatively a suspended substance from a given mass of water, the animal must, because of the constant mixing of the filtered with the unfiltered water, pass some of the water through its mantle cavity many times over, even should the water issuing from the exhalant siphon be completely cleared.

EXPERIMENTAL

In our work with the California sea mussel, *Mytilus californianus*, which unlike the *M. edulis* that inhabits bays, estuaries and river mouths, attaches itself to rocks and pilings near open, unprotected shores, we used some refinements of Dodgson's general method. We considered that serial measurements of a finely divided substance remaining suspended in a given mass of water in which mussels were immersed should provide approximate data regarding the rate of filtration of the water by the animals.

We have not overlooked the fact that individual animals may vary considerably in their relative rates of propelling water through their gill chambers; we have also considered the possibility that the rate of filtering by the animal may depend to a considerable extent upon such factors as (*a*) particle size, (*b*) concentration and (*c*) chemical nature of the chosen suspended material (i.e. whether of nutritional, inert, or injurious character), and the possible influence of such properties upon mucus secretion, ciliary motion, and frequency of closure of the valves.

For convenience in analyzing at intervals remaining suspended material, and in order to duplicate to some extent the conditions of nature, use was made of a calcareous marine mud, whitish to light grey in color, from Bird Key Harbor, Florida. In preliminary experiments² use was made of material which, according to Dr. E. M. Thorp, had passed through a 0.48-mm. mesh screen. Its introduction into water in which mussels were immersed had no perceptible influence upon the animals, which remained with valves apart and continued to filter water. Mussels when kept out of water for a short interval, then placed in a very turbid suspension of the mud, opened their valves without delay, and began "pumping" water. Figures 1-4 show a series of photographs illustrative of the rather striking clarification of turbid water in a relatively short time. Into each of two graduated cylinders, each containing

² These were undertaken in the early summer of 1935 by the senior author in collaboration with Dr. Roderick Craig of the Division of Entomology and Parasitology, University of California.

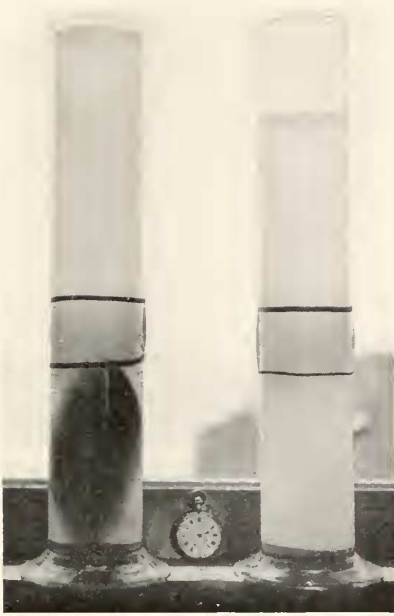


FIG. 1.

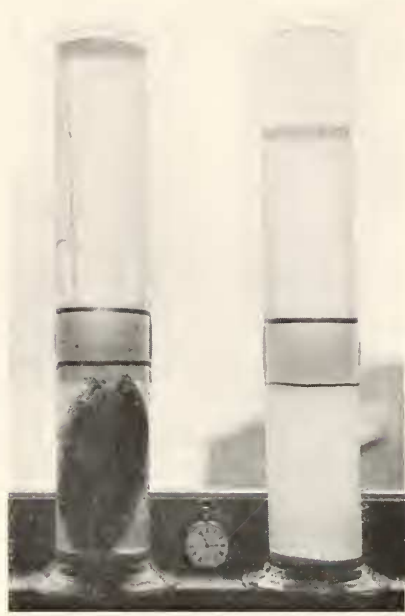


FIG. 2.

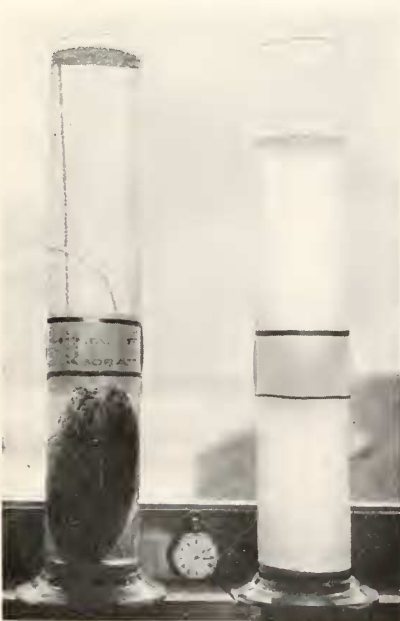


FIG. 3.

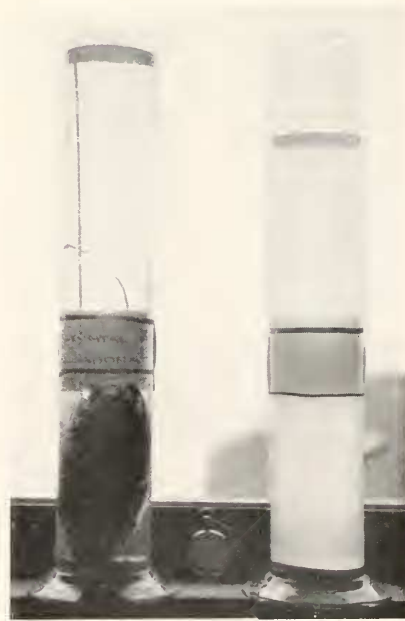


FIG. 4.

FIGS. 1-4. Removal of mud from suspension by a mussel. (Photographs by Dr. R. Craig.)

2,000 cc. of sea water, were placed 20 grams of the calcareous mud which was mixed with the water by several inversions of the temporarily stoppered containers. After the coarsest particles had settled out within a few minutes, the containers were placed in a window to afford good lighting, and a large mussel of 17 cm. length, and weighing about 485 grams, was placed in the one on the left side. The first photograph shows an identical degree of turbidity in the two suspensions at the beginning, as noted in the faint Tyndall beam from the edges of the cards strapped at the rear outer wall of each cylinder. In half an hour (Fig. 2), the turbidity in the mussel-containing jar had been greatly decreased, and the picture shows the printed letters upon the card, easily legible through the water. In 50 minutes (Fig. 3) the turbidity in the left container was all but gone, and in the last of the series (1 hour and 45 minutes) we see a perfectly clear solution. Note particularly the serial appearances of the string by means of which the animal had been lowered slowly into the container. The temperature of the collected sea water was initially about 20° to 21° C., and could have increased by not more than a degree or two.

Inspection of the sediment at the bottom of containers on the day following a filtration experiment revealed three types of precipitated mud: (1) very fine, homogeneous powder which had settled out by gravity; (2) piles of pseudofeces in the form of amorphous, stringy masses of material which had been filtered out by the mussel, incorporated in mucus, and expectorated from the mantle at the excurrent siphon; the extrusion of this material could be observed continuously from the beginning of the experiment; (3) true characteristic feces in the form of short, discrete, flattish straps composed of the mud which had been ingested by the mussel.

The intricate arrangements possessed by lamellibranchs for filtering the fine detritus and small organisms from water have been described and discussed extensively by other authors (Moore, 1905; Allen, 1914; Kellogg, 1915; Dodgson, 1928; Yonge, 1928; and others cited especially by the latter).

We know from the experiments reported in this paper and from previous ones (Fox et al., 1936) that the material filtered by the mussel from water may be in part swallowed (even if inert and nutritionally useless) and in part expectorated in mucus-laden strings or pseudofeces from the edges of the mantle, especially if the water contains a great amount of suspended matter. We were not in this particular study interested primarily in the relative quantities that were swallowed or rejected; we were interested in the rate of diminution of suspended material, and made preliminary measurements³ in order to learn (1) how

³ In the late summer of 1935 by the senior author jointly with Mr. Rae Schwenck, from the Department of Chemistry, Sacramento Junior College.

rapidly water may be propelled through the gill chamber of the mussel during such metabolic activities as feeding, respiration and excretion, and (2) how rapidly suspended organisms or other material may be removed from water, to be ultimately deposited in an altered state upon the bottom of the sea.

The results of these preliminary experiments were, however, not entirely satisfactory. Their difficulty of interpretation was doubtless due to the fact that we were at that time unaware of all the precautions which had to be taken in order to obtain results which could be readily analyzed.

The experiments were therefore repeated in the fall of 1936 (D. L. F. and J. P. C.), with the introduction of several refinements in technique and materials; these experiments will here be dealt with more fully. In the first of them the same calcareous mud was employed, but of a much finer grade, having passed (according to Dr. Thorp) through a 0.086 mm. mesh screen. The dry mud was shown by analysis to contain 1.66 per cent moisture, 90 per cent CaCO_3 , and 6 per cent SiO_2 (by difference). In later experiments, we used pure CaCO_3 instead, and found that it served equally well. (See below.)

In our experiments 8,000 cc. of fresh sea water, to which were added initially 32 grams of mud (4 grams per liter of water), were placed in each of a series of large battery jars. The suspensions were allowed to stand for about one hour, to allow time for larger aggregates of mud particles to settle to the bottom.

The mussels were handled carefully throughout the work; they were placed on the table for a time with the valve openings vertical to the surface, in order to allow the water within the mantle cavity to drain out when the animals opened their shells; this not only prevented changes in the volume of water introduced into the containers, but probably rendered the animals sufficiently "thirsty" to insure their commencing activities almost directly they were immersed in the suspensions; the prompt opening of their valves after immersion could be recognized by bubbles of displaced air rising to the surface, and often also by watching the animals which lay close to the glass walls of the jars. A moderate stream of air was introduced through a glass tube reaching to the bottom of each jar, sufficient to insure constant homogeneous mixing without disturbing the animals or stirring the heavier material which was deposited on the bottom by ordinary settling or by the animals.

Although the animals kept their valves apart during the course of the experiments, it was observed, by following the course of suspended particles, that the currents of water flowing into the incurrent and out of the excurrent siphon were not of continuous intensity, but occurred

at apparently rhythmical intervals, the intensity of the stream alternately increasing to a maximum, then gradually diminishing to a mini-

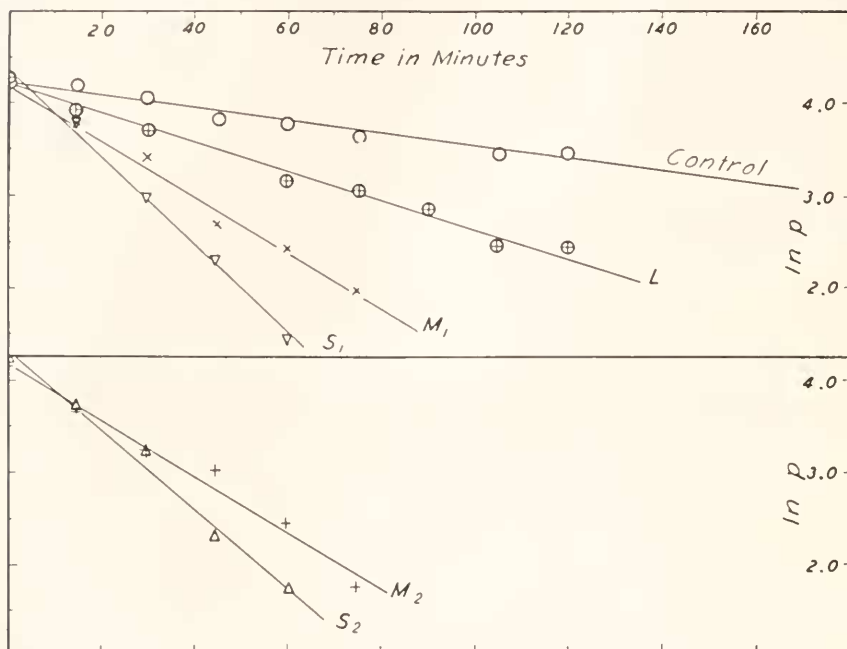


FIG. 5. Removal of suspended CaCO_3 by mussels; first series.

First Series:

- Large mussels— 2 animals. Lengths 130 mm. and 110 mm. (average = 120 mm.).
Total weight 333 grams (average = 166.5 grams) each.
- Medium mussels—(M_1) 4 animals. Lengths 97, 100, 100 and 103 mm. (average = 100 mm.).
Total weight 302.5 grams (average = 75.6 grams) each.
- (M_2) 4 animals. Lengths 95, 95, 105 and 105 mm. (average = 100 mm.).
Total weight 299.4 grams (average = 74.8 grams) each.
- Small mussels—(S_1) 9 animals. Lengths 70, 78, 67, 73, 76, 72, 75, 74 and 65 mm. (average = 68.9 mm.).
Total weight 308.4 grams (average = 34.4 grams) each.
- (S_2) 9 animals. Lengths 78, 69, 79, 75, 82, 79, 60, 62 and 82 mm. (average = 74 mm.).
Total weight 360.0 grams (average = 40 grams) each.

Ten-cc. samples taken every 15 minutes. Temperature range 22.85° to 23.4° C.

num. This could be observed particularly well in the large mussels. Mucus-laden strands of the filtered mud were expelled at a slow but

nearly constant rate from the edges of the mantle at the exhalant opening. These pseudofeces either fell rapidly to the bottom, or, if attached to an air bubble or two, rose to the top. They did not break down and become redispersed.

Samples were removed at stated intervals (10 or 15 minutes) from a uniform place in the center of the container and at about the mid-depth point, with calibrated 10-ml. pipettes, and introduced into stoppered vessels for analysis. These samples were acidified before washing them into containers for analysis, in order to insure that none of the colloidal CaCO_3 material remained adsorbed to the walls of the vessels. The microchemical method of Kirk and Moberg (1933) for the analysis of

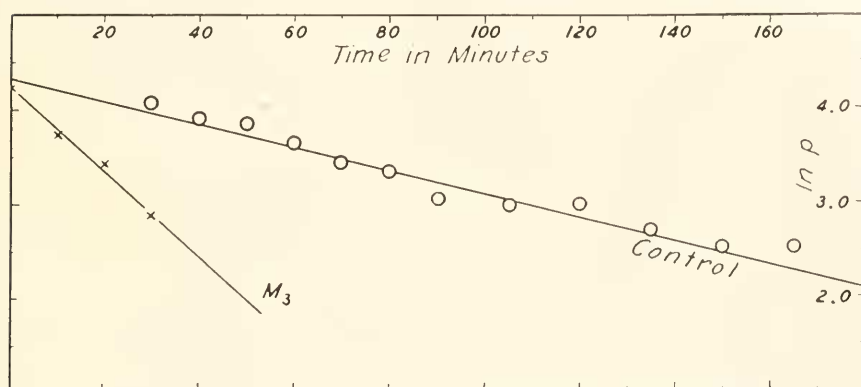


FIG. 6. Removal of suspended CaCO_3 by mussels; second series.

Second Series:

Six mussels used.

Medium (M). Lengths 98, 108, 100, 103, 105, 107 mm. (average = 103.5 mm.).

Total weight 611.5 grams (average = 102 grams).

Ten-cc. samples taken. Temperature range 20.8° to 21.35° C.

calcium in blood or sea water was employed. The calcium is precipitated as the oxalate, washed, and titrated in acid solution with standard potassium permanganate. By this method the amount of calcium is determined with an accuracy of ± 4 mg./liter. The concentration of dissolved calcium in the ordinary sea water used in these experiments was determined by the same method.

Controls (i.e. jars containing identical quantities of water and suspended mud, with similar moderate aeration but without mussels) were always carried out, parallel with the experiments, and samples were taken from these at the same intervals.

Two series of experiments (Numbers 1 and 2) were undertaken using the calcareous marine mud; the results are shown in Figs. 5 and 6.

The data for these figures were collected and originally tabulated in exactly the way shown in Table III.

Two series of experiments (Numbers 3 and 4) were also performed with the use of pure, finely divided CaCO_3 ; the results are recorded in Figs. 7 and 8 (from data tabulated as in Table III, which shows data from which Fig. 8 was derived). Freshly collected specimens were

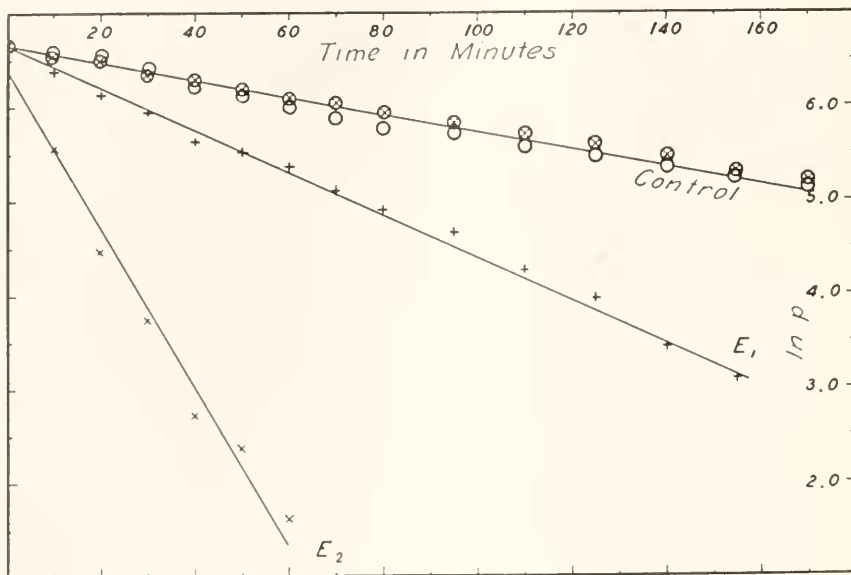


FIG. 7. Removal of suspended CaCO_3 by mussels; third series.

Third Series:

Very large mussels.

E_1 . Two animals. Lengths 179 and 174 mm. (average = 176.5 mm.).
Weights 434.7 and 395 grams respectively (average = 415 grams).

E_2 . Two animals. Lengths 182 and 178 mm. (average = 180 mm.).
Weights 337 and 400 grams respectively (average = 368 grams).

Ten-cc. samples taken. CaCO_3 used; 2 grams/liter (16 grams total) in each tank. Temperature range 18°–20° C.

used in these experiments. Placed carefully in the containers, they soon opened their valves, and showed no objection whatever when the carbonate was added, but continued to filter the water in a normal manner.

In one experiment (see Fig. 7) two pairs of very large mussels, collected at an exceptionally low tide, were employed. These individuals were selected from the catch on the basis of fair uniformity of size and their readiness to open their valves and propel water without showing

cessation of activity or other disturbed responses to slight mechanical stimuli such as stirring the water in which they were immersed, or tapping upon the container.

Four jars were set up, each containing 6 liters of sea water. Two selected mussels were placed in each of two jars while the other jars were left as controls. Air was passed at a uniform rate through each jar of water as before. After all four of the animals had parted their valves, the additional two liters of water were added to each jar (to make up the total of 8 liters), the suspended CaCO_3 being added with the water in the operation.

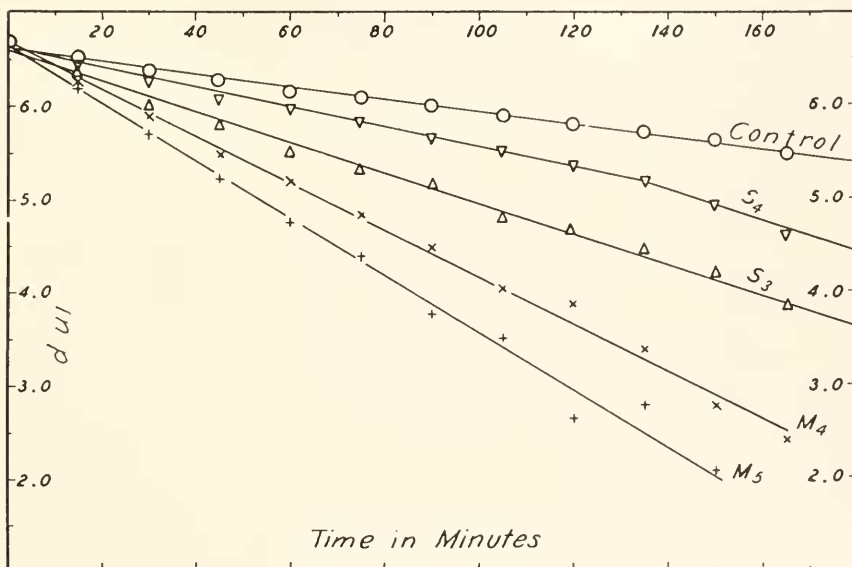


FIG. 8.

The "zero points" of the two control jars (without mussels), which agree very closely, were obtained by taking samples immediately after adding the CaCO_3 in the regular manner and are taken to serve as initial points for the duplicate experiments as well, since identical quantities of the salt had been added to the same volumes of water under the same conditions, and previous experiments had shown good checks in the initial quantities of suspended material under such conditions.

Table III shows data relating to duplicate experiments on (1) medium-sized mussels (M_4 and M_5) and (2) small mussels (S_3 and S_4) all run simultaneously along with a control (C). Four mussels were placed in each jar, and the experiments were conducted in a manner

identical to the previous set. Again, the initial value for suspended CaCO_3 in the *control* jar was taken to represent a reliable figure for that of the experimental jars.

In these experiments wherein CaCO_3 was used, it is noted that although the initial quantity of CaCO_3 suspended in the water exceeds by an average of some ten-fold the quantity suspended when the calcareous marine mud was employed in the earlier experiments, nevertheless the

TABLE III

Removal of suspended CaCO_3 by mussels—fourth series. Medium mussels: M_4 —4 animals. Lengths 105, 100, 102 and 109 mm. (Average = 104 mm. each). Total weight 342.5 grams (Average = 85.6 grams each). M_3 —4 animals. Lengths 106, 104, 102 and 108 mm. (Average = 105 mm. each). Total weight 337.5 grams (Average = 84.4 grams each). Small mussels: S_3 —4 animals. Lengths 78, 79, 77 and 74 mm. (Average = 77 mm. each). Total weight 139 grams (Average = 34.75 grams). S_4 —4 animals. Lengths 75, 81, 74 and 77 mm. (Average = 77 mm. each). Total weight 156 grams (Average = 39 grams each). Ten-cc. samples taken. Temperature range 19° – 20.3° C. CaCO_3 used. Two grams per liter (Sixteen grams total in each tank).

Time	Minutes	Control C	Medium M_4	Medium M_3	Small S_3	Small S_4
		Ca	Ca	Ca	Ca	Ca
		grams/liter	grams/liter	grams/liter	grams/liter	grams/liter
1:15 P.M....	0	1.2356	—	—	—	—
2:10 P.M....	15	1.1185	.9542	.9314	1.0142	1.1000
2:25 P.M....	30	1.0171	.7828	.7271	.8385	.9542
2:40 P.M....	45	.9585	.6714	.6142	.7571	.8642
2:55 P.M....	60	.8928	.6057	.5457	.6771	.8214
3:10 P.M....	75	.8685	.5543	.5114	.6371	.7642
3:25 P.M....	90	.8242	.5185	.4728	.6000	.7200
3:40 P.M....	105	.7828	.4871	.4628	.5500	.6814
3:55 P.M....	120	.7528	.4771	.4443	.5343	.6428
4:10 P.M....	135	.7300	.4585	.4457	.5143	.6085
4:25 P.M....	150	.7028	.4457	.4385	.4957	.5671
4:40 P.M....	165	.6685	.4414	.4243	.4771	.5314
4:55 P.M....	180	.6500	.4343	.4257	.4685	.5143

rate of removal of suspended material by mussels of from 69 to 105 mm. in length is similar in both series of experiments. (See Table IV.)

The total calcium content represents the sum of the amount of calcium which is present in solution in the sea water and the added amount which is present in suspended material. The decrease of the calcium content with time is due to:

1. Gravitational settling of suspended material.
2. Removal (filtration) of suspended material by the mussels.

In the control experiments, which were undertaken without mussels in the vessel, the decrease was due to gravitational settling only, and a

general law can be found for the rate of this settling. During the experiments with mussels in the vessel, the decrease was due partly to settling and partly to removal of the material from suspension by the mussels; knowing the former, the rate of removal of the calcium by the mussels can be determined by difference. In all cases the mussels decreased the calcium content to a minimum value of about 430 mg. Ca per liter, whereas a determination of the contents in water filtered through paper gave about 440 mg. Ca per liter. Additional unpublished experiments have shown that a small amount of the calcium in the water, present probably in a very finely suspended state, could be filtered by the mussels but was not filtered out by paper alone, previous to analysis. It

TABLE IV
Liters of water passed per mussel per hour.

Series No. and value of a	Experi- ment No.	Size of mussel		Number of mussels	Value of b	m in liters per hour
		Mean weight	Mean length			
(1) 0.39	1	166.5	120	2	0.93	2.2
	2	75.6	100	4	1.81	2.8
	3	74.8	100	4	1.82	2.9
	4	34.3	69	9	2.80	2.1
	5	40.0	74	9	2.57	1.9
(2) 0.70	6	101.9	103.5	6	2.59	2.5
(3) 0.54	7	415	176.5	2	5.05	18.1
	8	368	180	2	1.36	3.3
(4) 0.41	9	85.6	104	4	1.51	2.2
	10	84.4	105	4	1.85	2.9
	11	34.8	77	4	0.98	1.1
	12a	39.0	77	4	0.65	0.5
	12b	39.0	77	4	1.02	1.2

appears therefore justifiable to assume that the content in solution was about 430 mg. Ca per liter and that *the suspended amount was equal to the observed value minus 430 mg. Ca per liter.* The value 430 may be in error by about 1 mg./liter whereby a slight uncertainty is introduced as to the amount of suspended calcium, and this uncertainty exerts a corresponding slight influence upon the further treatment of the data, since this has to be based upon the *suspended* amount of calcium and not upon the total amount.

By plotting the results from the control experiment one obtains a curve of a form which suggests that in the absence of mussels the amount of suspended calcium can be expressed as an exponential func-

tion of time. We assume, therefore, that the amount which is precipitated in unit time is proportional to the total amount which is suspended. If we have in the vessel M liters of water containing p mg. of suspended calcium per liter, the amount precipitated in unit time will be aMp , where a is a factor of proportionality. The amount precipitated in the time dt will be:

$$(a M p dt)$$

Concerning the action of the mussel, we will assume that *in unit time each mussel pumps m liters of water through its system and removes all suspended calcium from this quantity of water.* The amount removed by one mussel in unit time will then be $m p$, and if we have n mussels the amount of suspended calcium removed in the time dt will be:

$$(n m p dt)$$

The total amount removed owing to both ordinary precipitation and to the action of the mussels, representing the total decrease of the suspended amount of calcium, is therefore:

$$(1) \quad d(M p) = - (nm + aM) p dt$$

where the minus sign indicates a decrease. Therefore;

$$\frac{dp}{p} = - \left(\frac{nm}{M} + a \right) dt = - b dt$$

$$(2) \quad \ln p = - \left(\frac{nm}{M} + a \right) t = - bt$$

$$(3) \quad p = p_0 e^{-\left(\frac{nm}{M} + a\right)t} = p_0 e^{-bt}$$

The logarithmic decrement a can be determined from the control experiment and the logarithmic decrement b from the experiments with mussels. The amount of water which passes through one mussel in unit time is then:

$$(4) \quad m = M \frac{b - a}{n}$$

If our assumptions are correct, each experiment must reveal a linear relationship between the natural logarithm of p (the amount of suspended calcium in mg. liter) and the time. Furthermore, we must obtain nearly the same values of p_0 , the amount of suspended calcium at the beginning of the experiment, since in each case the initial conditions were as similar as possible.

In order to examine this question, the values of p have been computed by subtracting 430 mg./liter from the observed values of the total calcium content. All values of p smaller than 5 mg./liter have been omitted (except in one instance when a value of 4.3 mg./liter has been retained) since, owing to the slight uncertainty involved in the micro method for determining the amount in solution (430 mg./liter), small values of p have no significance. In the case of the control experiments values only from the first three hours have been considered, although p remained greater than 5 mg./liter.

In Figs. 5, 6, 7, and 8, the values of $\ln p$, as derived from the four series of experiments, have been plotted against time. The straight lines represent lines of regression which have been computed by the method of least squares. It is seen that all points fall so near to the lines that the deviations may be considered accidental. Accidental deviations must arise, since the samples taken from the middle of the jar cannot be expected to show exactly the average contents of suspended calcium, and since errors of determination are present. In the case of the small mussels (S_4), in series No. 4, a break in the line appears to occur after 130 minutes, indicating that the rate of propulsion of water through the mussels suddenly changed.

From the control experiments, we obtain various values of our constant a , using one hour as the unit of time (see Table IV). The variation of the values of a may be due to differences in the velocity of the stream of air which was passed through the water in order to insure homogeneous mixing, or, to a lesser extent, to differences in the effect of the salt water in coagulating the suspended material. In all experiments, however, the velocity of the air stream was adjusted so that the rate of bubbling through control jars and experimental jars was as closely identical as estimation would permit.

From the experiments with mussels we find the values of b which are shown in Table IV and the values of m (in liters per hour) which have been computed by means of formula (4), introducing M (8 liters), the number of mussels (n), and the value of a which was found by simultaneous control experiment.

The fact that in all cases we find a linear relationship between $\ln p$ and time appears to furnish strong evidence for the correctness of our assumptions, but from our equations it is evident that we should obtain a linear relationship on other assumptions than these which have been introduced. We could assume that the mussels remove only a constant fraction of the suspended calcium when m liters pass through the mussel. The amount removed would then be $cnm p$, where c must be sup-

posed to be a constant factor smaller than 1.0. It appears, however, improbable that a mussel should remove, say, 50 mg./liter when the content was 100 mg. liter and in the same interval of time, 2 mg./liter when the content was 4 mg. liter. A change in the ratio of the removed calcium from say 80 per cent of a high content to 100 per cent of a small content is, however, possible and would not be detected. If such a change takes place, our values of m are conservative, being somewhat low. Another conceivable possibility which may be mentioned is that the amount of water passing through the mussel chamber might decrease with time and the fraction of calcium removed might increase (or vice versa). However, the product mp must, since $\ln p$ is a linear fraction of time, remain nearly constant, and this means that the amount of water passing through the mussel chamber and the fraction of calcium removed would have to change in opposite directions at the same rate. It is difficult to conceive a mechanism which would work in such a manner. The simplest explanation of our results appears to be that our original assumptions are correct, viz., that a constant amount of water passes through the mussel chamber in unit time and that virtually all suspended (and colloidal) calcium in this amount of water is removed.

We have furthermore supposed that the water passing through the mussels has the average calcium content of the water in the vessel. In order to satisfy this condition, the water must be stirred, since the mussels lying on the bottom of the vessel remove practically all suspended calcium from the water passing through them. The stirring must be adapted to the number of mussels; the greater this number the more rapid must the stirring be. The effect of insufficient stirring upon the observations would be that $\ln p$ would no longer be a linear function of time, but would decrease more and more slowly as the experiment advanced. The reason for this is that the amount of suspended calcium removed by the mussels would no longer be proportional to p , but since the bottom layer, where the mussels lie, would be depleted of calcium more rapidly, it would be proportional to some function of p which decreases with time. We can introduce

$$nm p e^{-ct} dt$$

instead of

$$nm p dt$$

and obtain

$$\ln p = \ln p_0 - at - \frac{nm}{Mc} (1 - e^{-ct})$$

At great values of t , we obtain

$$\ln p = \ln p_0 - \frac{nm}{Mc} - at,$$

meaning that the decrease in the calcium content approaches the value which is due to gravitational settling only. The coefficient c which has been introduced depends upon the rate with which water passes through the mussels and upon the rate of stirring, and a determination of this coefficient is hardly possible. A computation therefore cannot be based upon the results of such experiments. During the experiments which are dealt with here, the water was stirred by passing through a constant stream of air, and the agreement between observed and computed values shows that the stirring was sufficient.

Two preliminary experiments which Fox and Schwenck undertook in the summer of 1935 with two very large mussels weighing 485 and

TABLE V
Rates of water propulsion by mussels.

Weight of mussels		Length of mussels		Number ex- periments	Total no. mussels used	Rate of water propulsion	
Range	Average	Range	Average			Range	Average
<i>grams</i>	<i>grams</i>	<i>mm.</i>	<i>mm.</i>			<i>liters/hr.</i>	<i>liters/hr.</i>
337-515	431	174-182	178	4	6	1.8-18.1	6.4
75-166	93	95-130	102	6	24	2.2- 2.9	2.6
34- 40	37	60- 82	74	4	26	0.5- 2.1	1.4

515 grams show a wider scattering of the observed values, but they indicate a linear relationship between $\ln p$ and t , giving m equal to 1.8 and 2.4 liters per hour respectively.

Other preliminary experiments by Fox and Schwenck, in the summer of 1935, gave less consistent values. In these experiments a large number of small mussels were used and $\ln p$ decreased rapidly at the beginning, but slowly at the end of the experiments, probably because the stirring was insufficient.

The results of all experiments, including the preliminary ones by Fox and Schwenck, are summarized in Table V. The very large mussels show an enormous range in their rate of water propulsion, perhaps owing to individual differences or perhaps because they work intermittently. The value obtained from one of the experiments, 18.1 liters per hour, is quite enormous, but it is undoubtedly correct since it is based on good observations during one full hour, and it shows that in certain cir-

cunstances large mussels can pump great quantities of water through their systems. The average value for the large mussels, 6.4 liters per hour, cannot be given any weight owing to the wide range of the single values and the small number of experiments. The medium-sized mussels appear to be more consistent in their behavior, the range of the single values is small and the average value, 2.6 liters per hour, can therefore be considered nearly correct. The small mussels show again a wider range of their rate of water propulsion and while the average value is uncertain, it undoubtedly lies below that of the larger animals.

It would be expected that both the weight and the volume (capacity of the gill chamber) of the mussel should be proportional to some fairly constant power of one of the linear dimensions, say the length of the shell, and that weight should show a linear relationship to capacity. The capacity (in ml.) was determined by allowing mussels whose gill chambers had been emptied of sea water to refill their cavities on immersion in a known volume of sea water, then causing the animals to close their valves, removing them from the vessel, and measuring the residual water in the container. Plotting the average lengths of a series of different sized animals (in mm.) against their capacities (in ml.) showed a steeply rising curve of an exponential character; length plotted similarly against weight of animals (in grams) emptied of water showed a curve of similar character (see also Galtsoff, 1931, who obtained a similar relationship in the Hawaiian pearl oyster); finally the relationship between weight and capacity was shown to be a linear one.

An extensive series of experiments performed upon mussels of different known capacities, weights, and linear dimensions would perhaps disclose an interesting relationship between any of these attributes (say the volume), and the rate of propulsion of water by each size of "pumping system."

SUMMARY

A method is described for determining the approximate average rate at which the California mussel, *Mytilus californianus*, propels water through its gill chambers.

The method consists of analyses at frequent intervals of the amount of calcium remaining in suspension (as CaCO_3) in a given volume of continually stirred water containing the mussels, which remove the suspended material as they pass the water through their chambers.

Mathematical treatment and interpretation of the data obtained, support the conclusions that (1) virtually all of the suspended matter is removed as the water passes over the mucous surfaces of the gills and mantle of the mussel; (2) the mussel propels the water rhythmically

through its filtering system at a rate which on an average is constant, varying according to the size and perhaps also according to other physiological attributes of the animals. In medium-sized animals (of 95 to 130 mm. length) the propulsion rate may vary between extreme values of 2.2 and 2.9 liters per hour, and has an average value of approximately 2.6 liters per hour.

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LITERATURE

- ALLEN, W. R., 1914. The food and feeding habits of freshwater mussels. *Biol. Bull.*, **27**: 127.
- DAMAS, D., 1935. Le rôle des organismes dans la formation des vases marines. *Ann. de la Soc. Géologique de Belgique*, **58**: 143.
- DODGSON, R. W., 1928. Report on Mussel Purification. Ministry of Agriculture and Fisheries. Fisheries Investigations, Series II, Vol. 10, No. 1.
- FOX, D. L., ET AL., 1936. The habitat and food of the California sea mussel. *Bull. Scripps Inst. of Oceanography, Tech. Ser.*, **4**: 1.
- GALTSOFF, P. S., 1926. New methods to measure the rate of flow produced by the gills of oyster and other molluscs. *Sci.*, **63**: 233.
- GALTSOFF, P. S., 1928a. The effect of temperature on the mechanical activity of the gills of the oyster (*Ostrea virginica* Gm.). *Jour. Gen. Physiol.*, **11**: 415.
- GALTSOFF, P. S., 1928b. Experimental study of the function of the oyster gills and its bearing on the problems of oyster culture and sanitary control of the oyster industry. *Bull. Bur. Fish.*, **44**: 1.
- GALTSOFF, P. S., 1931. The weight-length relationship of the shells of the Hawaiian pearl oyster, *Pinctada* sp. *Am. Nat.*, **65**: 423.
- GRAVE, C., 1905. Investigations for the promotion of the oyster industry of North Carolina. *Report, U. S. Comm. Fish.* 1903 (1905): 249.
- KELLOGG, J. L., 1915. Ciliary mechanisms of lamellibranchs with descriptions of anatomy. *Jour. Morph.*, **26**: 625.
- KIRK, P. L. AND E. G. MOBERG, 1933. Microdetermination of calcium in sea water. *Ind. and Eng. Chem., Analyt. Edition*, **5**: 95.
- MOORE, H. F., 1905. Anatomy, embryology, and growth of the oyster. *Report, U. S. Comm. Fish.* 1903 (1905): 317.
- MOORE, H. F., 1908. Volumetric studies of the food and feeding of oysters. *Bull. Bur. Fish.*, **28** (Part 2): 1297.
- MOORE, H. F., 1913a. Condition and extent of the natural oyster beds and barren bottoms of Mississippi east of Biloxi. *Rep. U. S. Comm. of Fisheries*, 1911 (1913). Bur. of Fish. Document No. 774.
- MOORE, H. F., 1913b. Condition and extent of the natural oyster beds and barren bottoms of Mississippi Sound, Ala. *Ibid.* Bur. of Fish. Document No. 769.

- NELSON, T. C., 1921. Report of the Department of Biology of the New Jersey Agricultural College Experiment Station for the year ending June 30, 1920 (1921), p. 317.
- NELSON, T. C., 1935. Water filtration by the oyster and a new hormone effect thereon. *Anat. Rec.*, **64** (Suppl. 1): 68.
- PARKER, G. H., 1914. On the strength and the volume of the water currents produced by sponges. *Jour. Exper. Zoöl.*, **16**: 443.
- RANSOM, G., 1926. Le filtration de l'eau par les Lamellibranches et ses conséquences. *Bull. de l'Institute Oceanographique*, No. 469, p. 1.
- VIALLANES, H., 1892. Recherches sur la filtration de l'eau par les Mollusques et applications a l'Ostreiculture et à l'Océanographie. *Compt. rend. Acad. Sci.*, **114** (2): 1386.
- WELLS, W. F., 1916. Artificial purification of oysters. A report of experiments upon the purification of polluted oysters by placing them in water to which calcium hypochlorite has been added. Reprint No. 351, Publ. Health Reports, Vol. 31, No. 28. U. S. Publ. Health Service, p. 1848. Washington (cited by Galtsoff, 1928b).
- YONGE, C. M., 1928. Feeding mechanisms in the invertebrates. *Biol. Rev.*, **3**: 21.
- ZOBELL, C. E., AND W. A. LANDON, 1937. The bacterial nutrition of the California mussel. *Proc. Soc. Exper. Biol. and Med.* (in press).